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Sauropod dinosaur trackways in a Middle Jurassic lagoon on the Isle of Skye, Scotland

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Abbreviated title: Sauropod Trackways from Skye

Synopsis: The Middle Jurassic was a dynamic interval in dinosaur evolution, but the dinosaur fossil record from this time is extremely poor throughout the world. The Isle of Skye (Scotland) preserves marginal marine and terrestrial deposits of Middle Jurassic age, which have yielded sparse bones, teeth, footprints, and small segments of trackways belonging to dinosaurs. We report the discovery of the most extensive dinosaur fossil site yet known in Scotland: a coastal outcrop of the Duntulm Formation (Bathonian) at Cairidh Ghlumaig, Skye, that preserves numerous trackways of sauropod dinosaurs in multiple layers deposited in a lagoonal system. We present an initial description of these tracks and identify them as most likely belonging to a primitive, non-neosauropod species that retained a large claw on manual digit I and produced narrow-gauge trackways. They provide additional evidence that basal sauropods persisted deep into the Middle Jurassic, a time when the earliest members of larger and more derived sauropod lineages were radiating. The new Skye tracks document multiple generations of sauropods living with the lagoonal environments of Jurassic Scotland, and along with other tracks found over the past two decades, suggest that sauropods may have frequented such environments, contrary to their image as land-bound behemoths.

Introduction

The Middle Jurassic was a dynamic time in the evolution of dinosaurs, as the first tyrannosaurs and plate-backed stegosaurs, feathered theropods closely related to birds, and new types of colossal long-necked sauropods radiated while the continents drifted further apart. This story has been pieced together from sporadic fossils, because the Middle Jurassic is one of the most poorly sampled intervals in the 160+ million year evolutionary history of dinosaurs (Weishampel et al. 2004). Relatively few sites in the world preserve dinosaur fossils from this dark interval, ca. 174-164 million years ago. Any new discoveries, therefore, have the potential to reveal new species, fill in major gaps on dinosaur phylogenies, and help us better understand how dinosaur faunas were changing during this critical, yet poorly recorded, period of time.

One place where Middle Jurassic dinosaurs are preserved is Scotland. Although it is known that dinosaurs lived in Scotland during this time, much about their biology, habitats, and evolutionary relationships remains unclear. This is because the fossil record of Scottish dinosaurs is restricted to isolated bones (Benton *et al*. 1995; Clark *et al*. 1995; Clark 2001; Liston 2004; Barrett 2006; Wills et al. 2014; Brusatte & Clark 2015) and small portions of trackways, few of which have been found in situ (Andrews & Hudson 1984; Clark & Rodríguez 1998; Clark *et al*. 2004, 2005; Marshall 2005). These fossils, which are all from the Isle of Skye, show that several types of dinosaurs lived in Scotland between ca. 170-166 million years ago, including carnivorous theropods, long-necked sauropods, plant-eating ornithopods, and armoured thyreophorans. But beyond their basic identifications, little is known about these animals and how they functioned, interacted, and evolved during a time when Scotland was much warmer than today and covered by shallow seas, lagoons, and large rivers.

We report the discovery of a remarkable new dinosaur fossil site on the Isle of Skye: a coastal outcrop of the Duntulm Formation (Middle Jurassic: Bathonian) that preserves numerous trackways of sauropod dinosaurs, preserved in multiple stratigraphic layers and exposed along broad bedding planes. These are the first records of sauropod tracks from Scotland and augment the exceptionally poor fossil record of this major group of dinosaurs on Skye, which previously has been limited to a few isolated bones and teeth (Clark *et al*. 1995; Liston 2004; Barrett 2006). The new site is the largest known in situ dinosaur track locality in Scotland, both in terms of numbers of tracks and area of exposure. It provides important insight into the body size, environments, and locomotion of sauropod dinosaurs during the Middle Jurassic, an interval from which limited sauropod (or other dinosaur) fossils are known worldwide. Perhaps most fascinating of all, the Duntulm site illustrates how multiple generations of sauropods lived within the lagoon environments of Jurassic Scotland, an environment from which few dinosaur fossils have been found.

In this paper we present a short initial report on the new site, which serves to announce the discovery, provide a basic description of the tracks and their importance, and establish a first published record that can help ensure conservation of this globally-important Scottish dinosaur find. More detailed mapping and study of the site is ongoing and a comprehensive description will be published separately.

Geological Context

Mesozoic sediments of the Trotternish Penninsula of the Isle of Skye, Scotland, were deposited in the fault-bound Sea of the Hebrides Basin, which was juxtaposed to the south and east to the Inner Hebrides Basin in which contemporaneous sediments were deposited in the region that is now the Strathaird Peninsula of Skye. The two basins were separated by a topographic high known as the Skye High (Morton 1965; Hesselbo *et al*. 1998) but the degree of separation was insignificant by the time of deposition of the Great Estuarine Group, and time-equivalent deposits occur in each of the basins (Hudson and Andrews 1987).

The footprints described here occur in the Duntulm Formation of the Great Estuarine Group of the Sea of the Hebrides Basin. They were found at the type section of the Duntulm Formation on the foreshore of Cairidh Ghlumaig Bay (Figure 1a,b). This section is a Geological Conservation Review (GCR) site, known as "Duntulm (Cairidh Ghlumaig and Lon Ostatoin)", selected for its national importance for Earth heritage conservation (Cox and Sumbler 2002). It has a long history of study dating back well over half a century. Anderson (1948) described prominent algal limestones from this site, in units he termed the 'Lower Ostrea Beds'. The algal limestones were again discussed by Hudson (1970), who logged the section in great detail and produced the bed numbering scheme referred to by Andrews & Walton (1990) and used in this study. The Duntulm Formation was first formally named by Harris & Hudson (1980), superseding Anderson's (1948) 'Lower Ostrea Beds' in their review of the Mesozoic stratigraphy of the Hebrides. The age of the Duntulm Formation is not well constrained but the dinoflagellate and green algae palynomorph assemblage strongly supports a Bathonian age (see review in Brusatte *et al*. 2015). Furthermore, the presence of the bivalve *Praeexogyra* has been argued to imply a mid-late Bathonian age, though the distribution of *Praeexogyra* has been shown to be strongly controlled by facies (Hudson in Torrens 1980; Riding *et al*. 1991).

Following a brief description by Bell & Harris (1986), Andrews & Walton (1990) most recently worked on the Duntulm Formation at Cairidh Ghlumaig, conducting a comprehensive integrated study of the litho- and palynofacies. They recognised a sequence comprising well-bedded sandstones, shales and limestones that are abundantly fossiliferous and include the marine bivalves *Praeexogyra, Cuspidaria* and *Modiolus.* Fish fragments are common in certain horizons and include hybodont shark teeth and spines. The environment of deposition has previously been interpreted as a marine–brackish lagoonal complex that formed transgressively to cover the deltaic sandstones of the Valtos Sandstone Formation (Andrews & Walton 1990). Within the lagoon several lithofacies record deposition under different regimes. These range from brackish-marine conditions with the deposition of oyster shell banks (containing abundant fossils of the marine *Praeexogyra hebridica*: Price & Teece 2010) with argillaceous carbonate muds (Lithofacies 1 and 2 of Andrews & Walton 1990), supralittoral carbonate algal marshes (Lithofacies 3), sandstones from small prograding deltas (Lithofacies 4) and, in the upper horizons of the Duntulm Formation, muds and sands that yield a freshwater mollusc fauna and terrestrial pollen and spores.

The horizons yielding dinosaur prints and trackways are beds 9b, 34 and 35 (numbering system in Andrews & Walton 1990, Figure 1c). Beds 9b and 35 are calcarenites representative of lithofacies 4 and are interpreted to have been deposited under littoral conditions, whilst bed 34 is a limestone representing lithofacies 1, oyster shell banks deposited under marine conditions. The presence of prints in both these lithofacies testifies to the (temporary?) shallowness of water during deposition. Beds 9b, 34 and 35 do not possess any visible desiccation cracks, indicating the substrate was not aerially exposed at the time the dinosaurs walked upon it. Desiccation features, such as mud cracks, are commonly seen on other dinosaur footprint surfaces in the Valtos Sandstone and Kilmaluag Formations on Skye (e.g., Clark *et al*. 2005).

The structures described here are identified as dinosaur prints based on their consistent size, preservation of fine morphological features such as digits and claw marks, and their arrangement in orderly trackways (Figures 2–4).

Several lines of evidence rule out the possibility that these dinosaur tracks could be a type of concretion. We did not observe any concretions at the Cairidh Ghlumaig exposure, and concretions have not been reported from the Duntulm Formation previously (Morton & Hudson 1995). The deformation of the sediments under the tracks does not resemble that around a concretion, which is usually of limited vertical extent, and involves only low angle deflection of the bedding (Hudson & Andrews 1987:fig. 5b; Wilkinson 1993:fig. 3). By contrast, the deformation under the Duntulm tracks is more irregular, with variable angle (including high angle) deflection, and of larger vertical extent than might be expected for a concretion of comparable dimensions (Figure 4). Septarian calcite concretions up to about 1 metre across and 20 centimetres thick occur at several horizons within the Great Estuarine Group, most notably near the middle of the Lealt Formation in the upper Kildonan and lower Lonfearn Members (Hudson & Andrews 1987). However, the Duntulm dinosaur tracks lack any suggestion of septarian texture. Calcite concretions are also common within the thick sandstones of the Valtos Sandstone Formation. However, the Duntulm tracks lie within beds that are cumulatively only 45 centimeters thick, and in the Valtos Sandstone Formation sandstones less than 1 metre thick are nearly always fully cemented rather than concretionary (Hudson & Andrews 1987).

The tracks expressed as impressions (concave epirelief) bear some resemblance to soft sediment deformation structures, which are formed in unconsolidated sediment due to liquefaction, conventionally assumed to be associated with either earthquake activity (e.g. Ambrasays 1988) or rapid sedimentation of contrasting lithologies, e.g. sand overlying unconsolidated mud. At the Duntulm site, there is a conspicuous lack of lithological contrast within beds 34 and 35 (and the three sandstone beds below), and no indication that the sands of beds 34 and 35 are forming dewatering or liquifaction structures into the underlying strata. Additionally, the deformation structures underneath the tracks, which in some cases match the shape of the digits (Figure 4), would be unexpected in soft sediment deformation structures, as well as root traces or other structures relating to large plants.

Finally, the concave impression tracks also bear some resemblance to giant’s kettles (=potholes), which can be formed by eddy currents or glaciers. The presence of such structures in a coastal outcrop may not be unexpected. However, giant’s kettles typically have smooth and regular internal surfaces, not the more irregular margins of the Duntulm footprints. It would also be unusual for giant’s kettles to be concentrated in only a few layers on a large coastal outcrop, and to have the fairly uniform size and orderly spacing of the Duntulm tracks.

Description

Several isolated footprints (both sauropod and one very subtle and poorly-preserved tridactyl print, which may belong to an ornithischian or a theropod) have been recovered from bed 9b, but this is surely because only a small portion of this lithological unit is exposed as a bedding surface (Figure 3d). Trackways are present in bed 34 and are densely packed across the bedding surface. Most of these are composed of impressed (concave epirelief) prints, but there may be a few examples of filled tracks that stand out from the surface as a cast (convex hyporelief). The majority of prints at the site, and also the best preserved, occur in bed 35, as it is this layer that has the broadest exposed bedding plane. These include both concave epirelief and convex hyporelief prints, of the manus and pes, some of which are likely casts of the actual print rather than undertracks of deformed sediment (Figure 3a-c, e-h).

The largest sauropod pes prints are ca. 70 centimetres in maximum dimension, and where manus and pes prints are preserved together they exhibit a moderately high heteropody ratio, in which the area of the pes print is more than twice that of the manus print (ratio of ca. 0.35 for the best preserved manus-pes set: Figure 3e). The convex hyporelief prints often preserve fine anatomical details of digit shape and structure, but the concave epirelief prints are more poorly defined and resemble potholes, as fine details have been obscured by tidal erosion and/or are covered by barnacles and seaweed. These concave impressed prints are often surrounded by slightly raised rims of sediment on the bedding plane surface. When these can be seen in cross section, a ~20 centimetre deep zone of deformation is apparent below the print, which in some cases follows the shapes of the digits (Figure 4). In general, the pes prints are fairly uniform in size (ca. 50-70 cm in maximum dimension) and pes prints are at least as common as manus prints, unlike in some 'manus-only' sauropod tracksites (e.g., Lockley *et al*. 1994c; Falkingham *et al*. 2011 and references therein).

The manus prints are elliptical in shape, with a relatively straight posterior margin and a large impression for a claw on digit I (Figure 3e, g). No other digit impressions are clearly preserved. The pes prints expand in width anteriorly, but there are some morphological differences between them: some are nearly circular, whereas others are more elongated in the anteroposterior direction and either triangular or ovoid in shape. It is not clear if these differences indicate different trackmakers, locomotory styles, or substrate/preservational influences, but we suspect the latter. Some pes prints preserve traces of individual digits. The best preserved print exhibits four discrete digits (I-IV), all of which face approximately anteriorly (Figure 3a-c).

Other pes impressions have a similar arrangement and no pes prints have digits that are widely splayed laterally (Figure 3e-f).

Some of the prints in layers 34 and 35 clearly are organized into trackways (Figure 2). The spatial distribution of these trackways is complex, as several appear to be traversing each other, so the number and length of individual trackways remains to be confirmed by aerial mapping, as do precise measurements of stride length, pace length, and trackway width. Some of the trackways appear to extend for at least five metres. The best preserved trackway segments are narrow-gauge, with left and right pes prints overlapping on the midline (cf. Farlow 1992) (Figure 2c-d). The geometry of these trackways is very similar to narrow-gauge sauropod trackways from the Middle Jurassic of Oxfordshire, England (Day *et al*. 2004:fig. 7C).

Discussion

Identity of the trackmakers. The single tridactyl print from layer 9b (Figure 3d) may have been made by an ornithischian (possibly an ornithopod) or theropod, but distinguishing between the groups is difficult with only a single partially preserved print (Castanera *et al*. 2013). The other footprints are identified as sauropods due to the possession of several synapomorphies of the group: extremely large size, quadrupedal posture (manus and pes prints), an elliptical manus print impressed by a hand with metacarpals held in a semicircular arrangement, and pes prints impressed by a foot that widens anteriorly (Wilson 2005). Some stegosaurs have similar tracks to sauropods, but the large size and four prominent digits of the Skye footprints differentiate them from stegosaur prints, which are usually smaller and have three prominent digits (e.g., Whyte & Romano 2001). Within Sauropoda, the Skye prints can be assigned to the subgroup Eusauropoda based on the presence of a well-marked heel trace behind the pedal digits, which is indicative of a fleshy pad on the foot, a diagnostic feature of the group (Wilson 2005) (Figure 3a,e,f).

A more specific identity within eusauropod sauropods is difficult, because of the paucity of hand- and foot-related characters diagnosing major sauropod subgroups. Several lines of evidence, however, suggest that the prints probably belong to a fairly basal eusauropod that falls outside of the derived subgroup Neosauropoda (the clade including diplodocoids and titanosauriforms). Neosauropods possess a tightly bunched metacarpal colonnade that forms a broad arc when seen from above, an arrangement that is held to produce arched manus prints with a deeply concave posterior margin (Wilson 2005; Wright 2005). This is not seen in the Skye manus prints, which have a nearly straight to slightly convex posterior margin (Figure 3c, g). Additionally, the digits on the Skye pes prints face anteriorly, which differs from the laterally offset (curving) pedal digits of most sauropod footprints. The curved digits are regarded as a synapomorphy of either Neosauropoda (Bonnan 2005) or a closely related group (Wilson 2005). If the anteriorly straight digits of the Skye footprints are genuine, and not an artefact of preservation or substrate, then they suggest that the trackmaker retained a primitive (=plesiomorphic) foot morphology not seen in neosauropods.

Other features are also consistent with a non-neosauropod or basal neosauropod identification. The Skye prints exhibit a large impression made by the claw of manual digit I. A large claw is present in non-neosauropods and certain basal neosauropods (such as diplodocoids and basal macronarians), but is reduced or absent in the most derived neosauropods (Titanosauriformes: Day *et al*. 2002). The best exposed Skye trackways are narrow-gauge, a posture seen in the generally smaller non-titanosauriform sauropods such as non-neosauropods, diplodocoids, and basal macronarians (Farlow 1992; Wilson & Carrano 1999; Day *et al*. 2002, 2004; Wright 2005). In contrast, the larger and more derived titanosauriforms, as well as perhaps some particularly giant non-titanosauriforms, had wider-gauge trackways in which the left and right pes prints are widely separate on the midline (Farlow 1992; Wilson & Carrano 1999; Santos *et al*. 2009). The gauge of the Skye trackways remains to be confirmed by comprehensive mapping, and it must be noted that gauge measurements can sometimes be affected by preservation (e.g., Castanera *et al*. 2012). However, if genuine, the narrow-gauge trackways and the retention of a large manual claw indicate that the Skye trackmaker was not a titanosauriform.

Assigning the Skye sauropod prints to a particular ichnotaxon is difficult at present, and we withhold making any formal designation. With that said, the prints most close match the morphology of tracks classified in the "*Breviparopus*−like/*Parabrontopodus*−like" category of Avanzini *et al*. (2003) and Santos *et al*. (2009) (see also Lockley *et al*. 1994a; Marty *et al*. 2010). In common with these tracks, the Skye prints are narrow-gauge and exhibit moderately high heteropody ratios, the manus prints are crescent-shaped (not horseshoe-shaped), and the pes prints are wide with anteriorly directed claw marks (although it has been argued that at least some footprints of the *Breviparopus*/*Parabrontopodus* grade do not preserve claw marks: Marty *et al*. 2010). The Skye manus prints closely resemble manual tracks assigned to *Parabrontopodus* from the Early Jurassic of Poland (Gierliński 1997:fig. 1), Late Jurassic of North America (Santos *et al*. 2009:fig. 8I) and unnamed tracks from the Middle Jurassic of Mexico (Ferrusquía-Villafranca *et al*. 2007:fig. 11). The Skye pes prints are very similar in size and shape to *Breviparopus*-type pedal tracks from the Middle Jurassic of Yorkshire, England (Romano *et al*. 1999:fig. 3C; Romano and Whyte 2003) and the Middle-Late Jurassic of Morocco (Dutuit & Ouazzou 1980).

In summary, the sauropod footprints from Skye that have thus far been studied can be identified as similar to *Breviparopus*/*Parabrontopodus*-like footprints and most likely made by a primitive, non-neosauropod species. These preliminary identifications remain to be tested by a more comprehensive study of the site. Future study may show that more than one type of sauropod track type is present at the site, as is the case with the Oxfordshire tracksite which preserves trackways of both a narrow-gauge sauropod and a wide-gauge titanosauriform (Day *et al*. 2002, 2004). Further work will also better constrain the effect of substrate on the preservation of different track morphologies.

Implications for sauropod evolution. The Middle Jurassic was a key interval in the evolution of sauropods, as several major lineages that would radiate and achieve colossal size in the Late Jurassic and Early Cretaceous, such as the diplocodoids and titanosauriforms, began to diversity (Wilson 2002; Upchurch et al. 2004; Mannion 2010). Frustratingly, the Middle Jurassic is one of the most poorly sampled timespans during the evolutionary history of non-avian dinosaurs, with relatively few sites around the world preserving bones and teeth of sauropods and other species (Weishampel et al. 2004). The woefully incomplete sauropod body fossil record from this time indicates that many archaic non-neosauropod species, such as the mamenchisaurids in Asia and cetiosaurids in Europe, persisted alongside the very earliest neosauropods, including the fledgling members of the diplocodoid and titanosauriform lineages (Bonaparte 1979; Dong *et al*. 1983; Upchurch & Martin 2002, 2003; Alifanov & Averianov 2003; Remes *et al*. 2009; Mannion 2010). However, this patchy record leaves many questions unanswered.

The growing Middle Jurassic dinosaur footprint record is helping to augment the poor body fossil record, and is leading to a better understanding of sauropod evolution and turnover during this time. Important Middle Jurassic sauropod trackways are now known from England (Romano *et al*. 1999; Day *et al*. 2002, 2004; Romano & Whyte 2003), Mexico (Ferrusquía-Villafranca *et al*. 2007), Morocco (Dutuit & Ouazzou 1980), Portugal (Santos *et al*. 1994, 2009), and the United States (Foster et al. 2000). These localities show that many sauropods with different locomotory styles and hand/feet morphologies were present in the Middle Jurassic, with a greater diversity than is often indicated by the scrappy body fossil record. Some of the most spectacular sites, such as the vast Ardley Quarry site in Oxfordshire, also demonstrate that primitive non-neosauropod species with narrow-gauge locomotion were living alongside larger, more derived titanosauriforms that walked in a wide-gauge style (Day *et al*. 2002, 2004).

The new Scottish site is the most northerly Middle Jurassic sauropod tracksite currently known, and it provides further evidence of a relatively primitive sauropod with narrow-gauge locomotion, large thumb claws, and feet with straight digits persisting into the Middle Jurassic. It has been suggested that the few isolated sauropod bones and teeth previously reported from the Middle Jurassic of Skye have may have belonged to a primitive sauropod of the informal '*Cetiosaurus* grade' (Clark et al. 1995), although later workers argued that the fossils were too fragmentary to be certain (Liston 2004; Barrett 2006). The new tracksite confirms that non-neosauropod species lived in Scotland during the Middle Jurassic, just as they did in England, where they are represented by tracks (Romano *et al*. 1999; Day *et al*. 2002, 2004) and bones (Upchurch & Martin 2002, 2003).

Implications for sauropod biology and habitats. The new prints from Skye provide interesting information on the environments inhabited by sauropods. They record multiple groups of sauropods living and moving within a marine–brackish lagoon environment. Unlike bones and teeth, footprints cannot be transported, so their presence in the lagoonal facies of the Duntulm Formation is bona fide evidence of colossal, plant-eating dinosaurs being physically present in a Middle Jurassic lagoon system while alive. Because of the sheer number of footprints, and their occurrence in three distinct stratigraphic layers, the Skye site suggests that sauropods frequented lagoon systems in Middle Jurassic Scotland, possibly over a long period of time. The wide stratigraphic separation between beds 9b and 34/35 (5.3 metres) mostly likely represents several years of deposition, if not decades, centuries, or millennia. It appears, therefore, that multiple generations of sauropod dinosaurs called the ancient lagoons of Skye home. Whether these sauropods merely passed through the lagoons quite frequently or were habitually resident within them is difficult to determine.

The concept of lagoon-dwelling sauropods may seem at odds with the current portrayal of dinosaurs, and more in line with depictions of swamp-dwelling long-necked dinosaurs from a bygone era. It was once thought that sauropods were hopelessly heavy on land and needed to lounge in swamps to support their huge bulk, but this view fell out of favour with the Dinosaur Renaissance of the 1960s and 1970s, which used new evidence from dinosaur posture and growth data to reimagine sauropods as more dynamic creatures capable of walking competently, albeit slowly, on land (Bakker 1986). Several recent trackway discoveries, however, have shown that sauropods passed through, and possibly lived in, marginal marine settings, including tidal flats, carbonate ramps, and shallow lagoons (e.g., Pittman 1989; Lockley *et al*. 1994b; Dalla Vecchia 1998; Gierliński & Niedźwiedzki 2002; Day et al. 2004; Rylaarsdam *et al*. 2006; Ferrusquía-Villafranca *et al*. 2007; Santos et al. 2009; Thulborn 2012; Castanera et al. 2014; Marmi *et al*. 2014; Navarette *et al*. 2014).

The Skye site presents a confluence of evidence for sauropods living in the region of a submerged lagoon over multiple generations. The track-bearing units of the Duntulm Formation are well established as being formed in a marine–brackish lagoon (Andrews & Walton 1990). All track-bearing units lack desiccation cracks or other evidence of aerial exposure, unlike many trackways formed in marginal marine settings but on substrates that were aerially exposed due to low tides or sea level change (e.g., Day *et al*. 2004). Furthermore, the Duntulm beds preserving tracks also yield a great diversity of shark teeth and marine bivalves, demonstrating that the sauropod tracks were being made and preserved in the same environment as these clearly aquatic species. The multiple track-rich layers show that these environmental associations persisted for a long period of time. This fits with the general ichnofacies concept of Lockley *et al*. (1994b), who identified a common pattern of theropod and sauropod tracks (the latter referred to the ichnotaxon *Brontopodus*) in coastal plain carbonate systems, evidence that these animals were common inhabitants of such environments over long swathes of time.

It is tantalizing to speculate on why these massive, column-limbed, long-necked plant-eaters were living in Middle Jurassic lagoon systems. It may be that these lagoons provided a more abundant supply of food than more terrestrial environments. Where terrestrial plants are well preserved on Skye, within the Bajocian Bearreraig Sandstone Formation which directly underlies the Great Estuarine Group, the species diversity is low (Dower *et al*. 2004). Alternatively, living in lagoons may have helped the gigantic sauropods cool their bodies (which would be particularly important if they had high metabolisms as indicated by their fast growth rates: Sander *et al*. 2011), or afforded protection from predators, such as the fairly large theropod dinosaurs that left footprints in other exposures of the Duntulm Formation (Clark *et al*. 2004).

Whatever the reason, the Middle Jurassic sauropods of Skye were denizens of ancient lagoons, and perhaps this was a more widespread environmental preference for other sauropods.

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Figure Captions

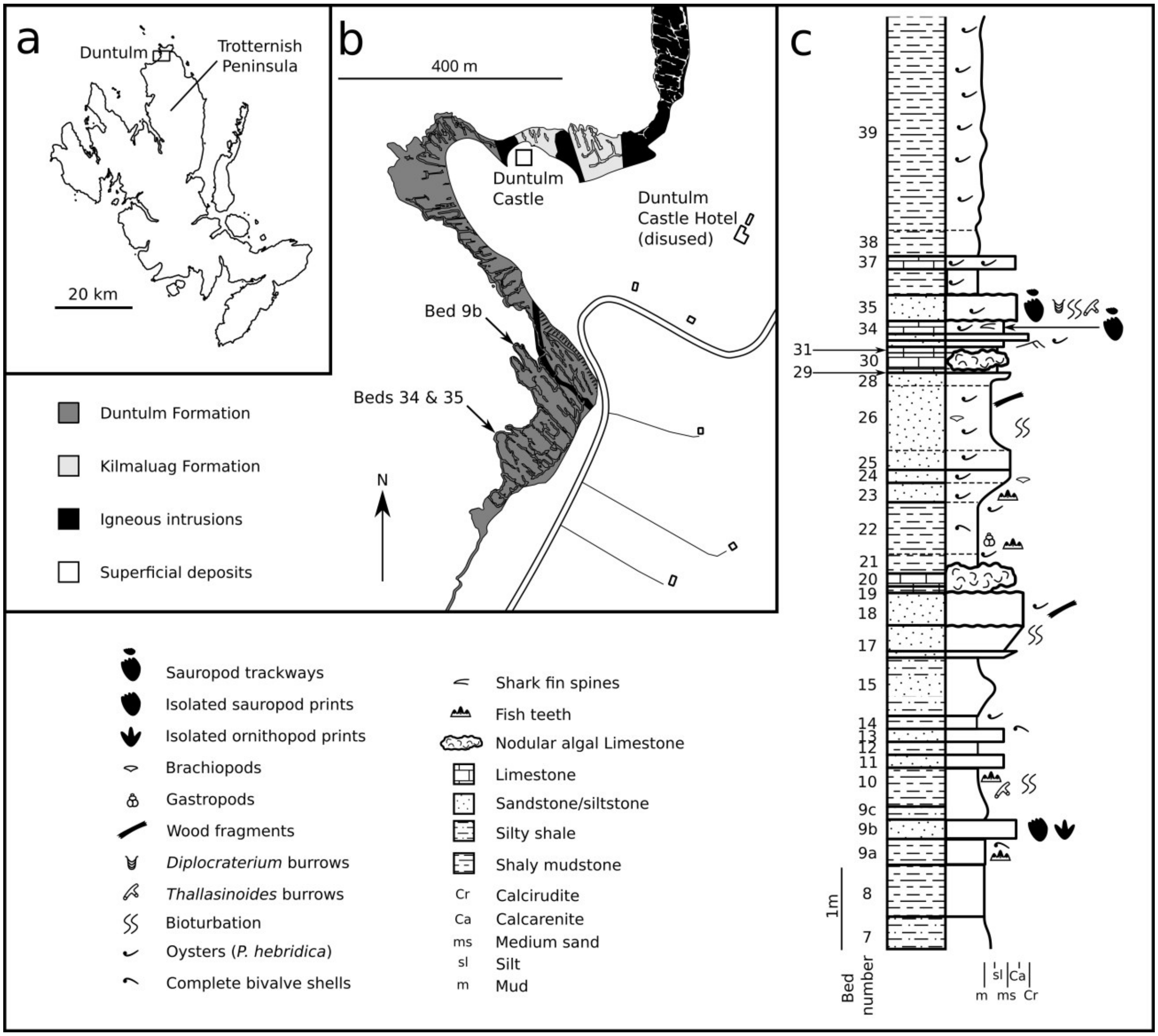


FIG. 1. Provenance information for the new Skye dinosaur tracksite (Cairidh Ghlumaig, Duntulm Formation, Bathonian). Map of Skye, Scotland, showing the geographic (**a**) and (**b**) geological context for the tracksite, and graphic log of the section at Cairidh Ghlumaig shore showing the horizons that preserve dinosaur footprints (**c**). Maps adapted from BGS 1:50,000 [Shapefile geospatial data], Scale 1:50,000, Tile: SC090, Version 2014, British Geological Survey, UK. Using: EDINA Geology Digimap Service, <http://edina.ac.uk/digimap>, Downloaded: April 2015.

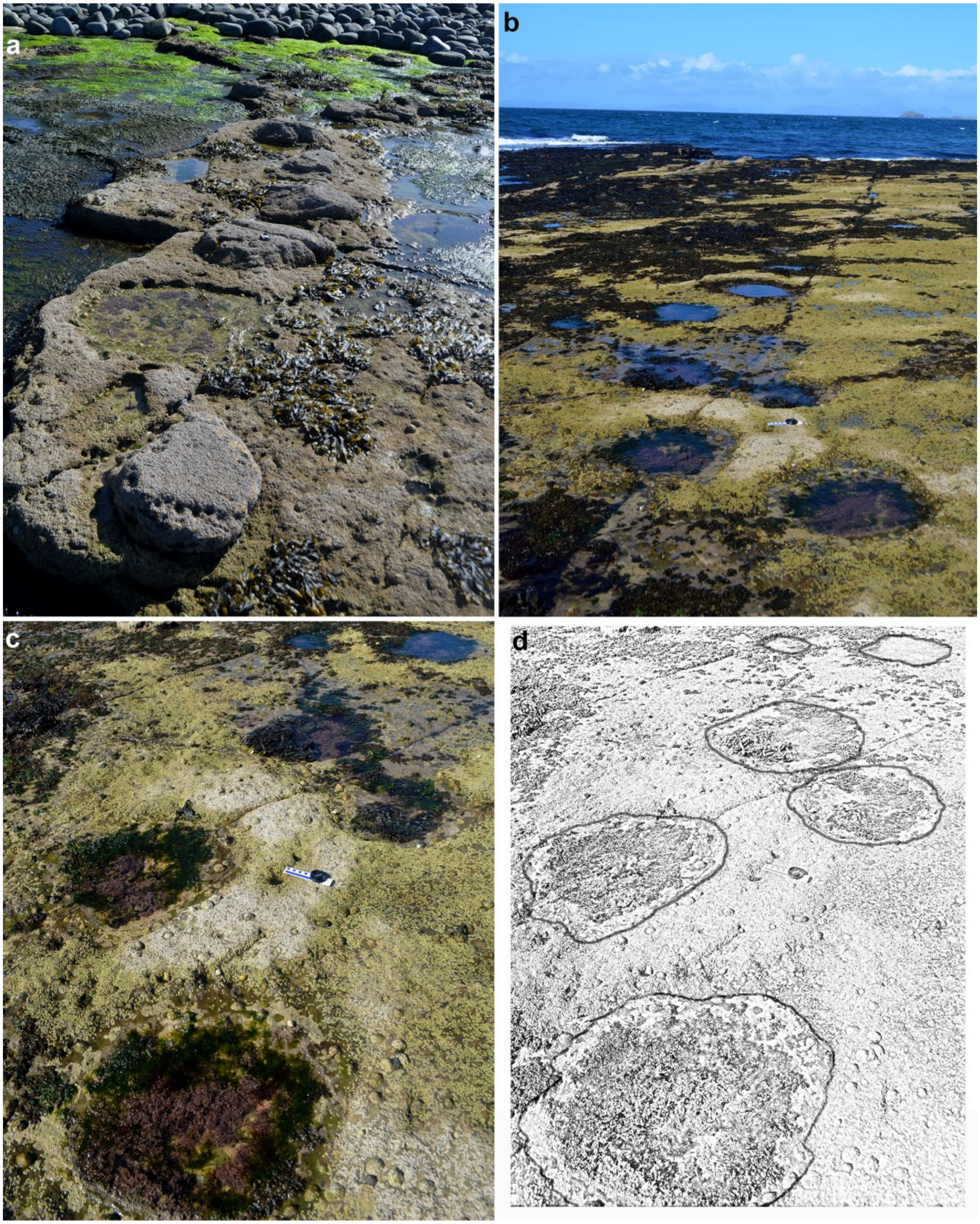
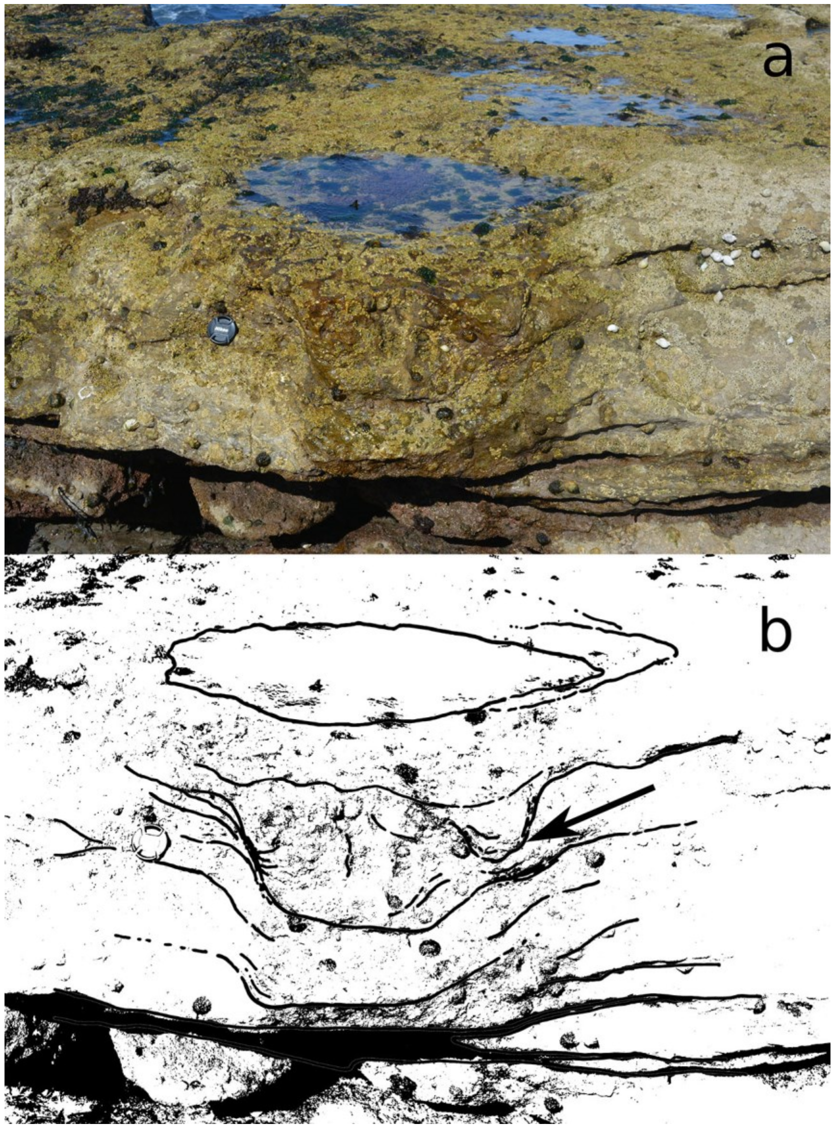


FIG. 4. Photograph (**a**) and line drawing (**b**) of a section of a sauropod footprint from bed 34 (Cairidh Ghlumaig, Isle of Skye, Scotland, Duntulm Formation, Bathonian) showing substrate

deformation below the bed surface. The arrow marks a region of isolated deformation within the deformed zone likely representing internal substrate deformation from the first digit claw. The original bed surface was the horizontal bedding plane above the claw mark. Diameter of lens cap equals 5 cm.

FIG. 3. Dinosaur tracks from the new Skye tracksite (Cairidh Ghlumaig, Duntulm Formation, Bathonian). (**a-b**). Photograph of well-preserved sauropod convex hyporelief pes print from bed 35. (**c**). Sauropod convex hyporelief manus and pes set in bed 35. (**d**). Photograph of tridactyl

footprint, with grey outline denoting the preserved edges of the print, from bed 9b (**e-f**). Sauropod convex hyporelief pes prints from bed 35. (**g**). Sauropod convex hyporelief manus print from bed 35. (**h**) Sauropod concave epirelief tracks from bed 35. Abbreviations: I-IV: pedal digits; Ic, manual digit I claw impression; m, manus; p, pes; pp, imprint of fleshy pedal pad. Diameter of lens cap equals 5 cm.



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